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Acknowledgments. We thank Mick Brand, Martina Ripcke and Ian Davidson for their enthusiasm and hard work in the field and lab; Matthew Norwood, CDU, for helping prepare equipment; Graeme Patch for organising use of drying ovens at DPI Berrimah; Dick Williams (CSIRO Darwin) for access to the Kapalga growth rate data; Jeremy Russell-Smith (Bushfire NT) for access to the "Three Parks" dataset. Saskia Grootemaat helped prepare several figures and Amy Zanne generated the phylogenetic tree. This work was made possible by funding from Macquarie University and from the Australian Research Council (DP120103284).

ABSTRACT

Plant growth rates strongly determine ecosystem productivity and are a central element of plant ecological strategies. For laboratory and glasshouse-grown seedlings, specific leaf area (SLA; ratio of leaf area to mass) is a key driver of interspecific variation in growth rate (GR). Consequently, SLA is often assumed to drive GR variation in field-grown adult plants. However, there is increasing evidence that this is not the general case. This suggests that GR – SLA relationships (and perhaps those for other traits) may vary depending on the age or size of the plants being studied. Here we investigated GR – trait relationships and their size dependence among 17 woody species from an open-canopy, fire-prone savanna in northern Australia. We tested the predictions that SLA and stem diameter growth rate would be positively correlated in saplings but unrelated in adults while, in both age classes, faster-GR species would have higher light-saturated photosynthetic rate (A_{sat}), higher leaf nutrient concentrations, higher branch-scale biomass allocation to leaf versus stem tissues, and lower wood density (WD). SLA showed no relationship to stem diameter GR, even in saplings, and the same was true of leaf N and P concentrations, and WD. However, branch-scale leaf:stem allocation was strongly related to GR in both age groups, as was A_{sat}. Together, these two traits accounted for up to 80% of interspecific variation in adult GR, and 41% of sapling GR. A_{sat} is rarely measured in field-based GR studies, and this is the first report of branch-scale leaf:stem allocation (analogous to a benefit:cost ratio) in relation to plant growth rate. Our results suggest that we may yet find general trait-drivers of field growth rates, but SLA will not be one.

Keywords: relative growth rate, specific leaf area, plant functional traits, leaf:stem allocation, leaf economic spectrum

INTRODUCTION

Growth rate differences between species are critical in determining the outcome of competition, while forest, shrubland and grassland yields – and carbon sequestration – are driven by growth rates. Since the 1970s, seedling relative growth rate (RGR; the dry mass increase per unit dry mass per unit time) has been treated as a key element of plant ecological strategies (Grime and Hunt 1975; Grime *et al.* 1997; Lambers and Poorter 1992; Lambers *et al.* 1998). A chief focus in that literature has been on identifying the key drivers of RGR variation. Although other formulations are possible (Cernusak *et al.* 2008; Enquist *et al.* 2007; Lambers and Poorter 1992), RGR is most commonly mathematically decomposed as follows:

$$RGR = NAR \times SLA \times LMF \; ; \qquad \text{(Eqn 1)}$$

where NAR is net assimilation rate (dry mass growth rate per unit leaf area), LMF is leaf mass fraction (leaf dry mass/plant dry mass), and SLA is specific leaf area (leaf area/leaf dry mass). A meta-analysis of 111 studies concerning herbaceous species found SLA to account for 64 % of RGR variation, whereas NAR and LMF accounted for just 26 % and 11 %, respectively (Poorter and van der Werf 1998). For woody species, meta-analyses have shown LMF has only a weak influence on RGR, with NAR and SLA being the dominant terms (Shipley 2006; Veneklaas and Poorter 1998). For seedlings, NAR variation is thought to largely reflect photosynthetic rate; for older plants, other factors presumably become increasingly influential on NAR, most especially carbon losses from tissue turnover, tissue respiration and root exudates (Konings 1989; Li *et al.* 2016; Poorter and Garnier 2007).

But do high SLA species achieve faster growth rates also as adults? Intuitively one might think so. After all, high SLA species typically have high leaf N and P concentrations and various other traits indicative of a “fast” lifestyle (Reich 2014). However, it seems

increasingly apparent that SLA and field-measured growth rates are most commonly unrelated (Aiba and Nakashizuka 2009; Coomes and Grubb 1998; Easdale and Healey 2009; Gower *et al.* 1993; Hérault *et al.* 2011; Martínez-Vilalta *et al.* 2010; Paine *et al.* 2015; Poorter *et al.* 2008; Rüger *et al.* 2012). In only a minority of cases – mostly for saplings or small trees – has a positive SLA-growth relationship been reported and even then, only weakly (Poorter and Bongers 2006; Prior *et al.* 2004; Reich *et al.* 1992; Rossatto *et al.* 2009; Wright *et al.* 2010). This raises the question, how is it that, through ontogeny – or with increasing plant size – variation in SLA becomes less strongly correlated with plant growth rate? This is an important question, with species-dimensions running from slow to fast growth rates, and low to high SLA, being widely accepted as pivotal in plant ecological strategies (Grime *et al.* 1997; Reich 2014; Westoby *et al.* 2002).

One potential explanation is that low SLA species accumulate more massive canopies over time (because of their longer leaf lifespans), and this counteracts their slower per-gram metabolic rates such that annual productivity can be as high as that of a high SLA species (Chabot and Hicks 1982; Matyssek 1986; Reich *et al.* 1992). Another potential explanation was outlined by Gibert *et al.* (2016). In their first-principles plant growth model, SLA always had a positive influence on growth rate but, as plants grow, this effect becomes increasingly masked by leaf turnover costs (which are higher in high SLA species, because of short leaf lifespans) and by increasing sapwood respiration costs – because larger plants have relatively more sapwood (King 1999; Poorter *et al.* 2012). Other predictions from this model were that, irrespective of plant size, light-saturated photosynthetic rate (A_{sat}) should correlate positively with growth rate, and wood density negatively. Meta-analysis across a range of trait – growth studies showed broad support for these predictions, though low sample size (number of studies) was a recurring problem for the analysis (Gibert *et al.* 2016).

Considering plant growth as an outcome of the balance between sapwood respiration and leaf photosynthesis is not new. For example, slower growth rates in larger (older) trees is likely a result of whole-plant sapwood volume increasing more rapidly over time than canopy leaf area (Ryan 1989). Of particular interest for the present study, one can make a related argument at branch-scale. That is, species (or indeed, individuals) deploying more leaf relative to stem wood and bark on terminal branches (i.e., with higher branch-scale LMF) should – all else equal – achieve faster whole-plant growth rates (Pickup *et al.* 2005). This intriguing proposition remains untested.

In this study we investigated the size-dependence of relationships between growth rate and several key plant functional traits (including branch-scale leaf:stem allocation), for a range of woody species from a fire-prone savanna in northern Australia. We chose this vegetation type because we expected the predicted relationships to be most clearly expressed in a situation where competition for light is minimal, and potential photosynthetic benefits are more likely to be realised. For each species we sampled traits both on small-DBH individuals and on larger-DBH individuals (henceforth called "saplings" and "adults"), and matched the trait data to previously reported long-term, stem-diameter growth rate data, re-calculated separately for small and large individuals. We tested the following predictions: (1) The GR – SLA relationship would be positive in saplings but absent among adult plants; (2) A_{sat} (expressed per unit leaf area) would explain substantial variation in GR, both in saplings and adults; (3) Trends in leaf N and P would mirror those in A_{sat} (e.g., because N-rich proteins and P-rich energetic molecules play key roles in plant metabolism); (4) Sapwood tissue density would be negatively related to GR both in saplings and adults; (5) Branch-scale leaf:stem biomass allocation would correlate positively with GR, both in saplings and adults.

MATERIALS AND METHODS

Trait dataset: site and species selection

We sampled species at Howard Springs Nature Reserve, 30 km east from Darwin. The savanna vegetation there is typical of the region, with an overstory dominated by eucalypts and an understory dominated by C_4 grasses. Overstory leaf area index ranges between about 0.6 in the dry season to 1 in the wet season (Hutley *et al.* 2001). At Darwin airport (20 km to the west), long-term annual rainfall is 1736 mm, typically with > 95% of rain falling during the wet season (October – April). Mean annual temperature is 27.6 ºC (data from www.bom.gov.au). Fires occur regularly in the dry season; typical fire return intervals in the region are 1 – 3 years (Russell-Smith *et al.* 2003). Soils at the site are sandy and low in nutrients: mean (and standard deviation) nutrient concentrations in eight soil samples (0-20 cm depth) collected in September 2010 were as follows: total C = 2.7 % (1.8), total N = 0.093 % (0.074), total P = 72.7 mg kg^{-1} (22.6).

Deciduous, semi-deciduous and evergreen species are all present in this savanna. Hence, we sampled plant traits at two time points: at the end of one dry season (September 2010), when deciduous species are leafless and the canopies of semi-deciduous species are at their thinnest; and right at the end of the subsequent wet season (early May 2011), when most species still tend to have full or nearly-full canopies (Williams *et al.* 1997). We selected 17 species to study, based on available growth rate data and their availability across two nearby sub-sites (12º27’10” S, 131º6’30” E; 12º27’57” S, 131º6’51” E). This species-set represents a range of functional types (trees and shrubs; nitrogen-fixers and non-fixers; deciduous, semi-deciduous and evergreen species; Table 1). We used diameter at breast height (DBH) to identify “adults” versus “saplings” for each species, but we use these terms informally (i.e., not necessarily reflecting degree of reproductive maturity), and synonymously with “small

individuals" and "large individuals" of each species (Prior *et al.* 2006). For species that are large trees at maturity we used a DBH cut-off of 6 cm to distinguish saplings from adults; for smaller trees and shrub species we used a 3 cm cut-off, with the exception of the small, short-lived and fast growing species *Acacia difficilis*, for which we used a cut-off of 1.5 cm DBH (Table 1). When choosing plants to sample we prioritised individuals of each species which clearly fell into these size-defined 'sapling' and 'adult' categories, so as to minimise ambiguity in this regard. For each age/size class of each species we aimed to make trait measurements on each of five individuals.

Leaf traits

Five recently-matured, fully-expanded and undamaged leaves (including petioles) were collected from each individual for determination of one-sided projected leaf area (flatbed scanner), oven-dried mass (70ºC for at least 48 hours), and thus SLA (area per dry mass; cm^2 g^{-1}). Total N concentration of leaf and soil samples was measured with a LECO TruSpec CHN analyser; total P by ICP-OES, on nitric acid digests (analyses run at Appleton Lab, University of Queensland). Area-based leaf N and P concentrations were calculated from mass-based concentrations and the mean SLA value for each species/age class.

Light-saturated rates of photosynthesis (A_{sat}) and stomatal conductance to water vapour (g_s) were measured during the wet season only, using a Li-Cor 6400XT portable infra-red gas analyser (5-8 replicate plants per species/age class). These measurements were made on leaves held on detached branches, > 1 m in length; branch-ends were re-cut and kept in water post-harvest until photosynthesis was measured (within 5 minutes of harvesting). Cuvette block temperature was kept at 26-27ºC, reference CO_2 was set to 400 ppm and cuvette photosynthetic photon flux density was maintained at 2000 μmol m^{-2} s^{-1}. Cuvette

145 vapour pressure deficit was only loosely controlled, averaging 1.22 kPa across all
146 measurements (standard deviation 0.28). Leaf lamina material used in photosynthetic
147 measurements was oven-dried and pooled per species/age class, then analysed for $^{13}C/^{12}C$
148 stable isotope composition (hereafter "$\delta^{13}C$") at the Stable Isotopes Laboratory, Australian
149 National University, Canberra. The $\delta^{13}C$ provides an integrated measure of the extent of CO_2
150 drawdown during photosynthesis (Farquhar *et al.* 1982). We also measured $\delta^{13}C$ on
151 representative whole-leaf (including petiole) samples collected during September 2010 (dry
152 season).

153

154 *Branch traits*

155 A single terminal branch, 80 cm in length, was sampled from each of several individuals of
156 each species/age class (average, 4.8 branches per species/age). These were divided into
157 segments cut at 5, 10, 20, 40 and 80 cm from the terminal end, and oven-dried at 70ºC for at
158 least 5 days. For each 80 cm branch (and including material on any side-branches) we
159 calculated (1) total leaf dry mass, (2) total stem dry mass, (3) the ratio of leaf:stem dry mass
160 for this 80cm segment (hereafter LM:SM), (4) the ratio of leaf *area*: stem dry mass (by
161 multiplying leaf mass by the appropriate SLA value; hereafter LA:SM), and (5) the allometric
162 slope describing leaf mass accumulation versus stem mass accumulation (hereafter
163 a_LMSM). This slope was estimated for accumulations from the tip going back down the
164 stem, expressed at the 5, 10, 20, 40 and 80 cm sampling points. These allometries were
165 calculated as standardised major axis slopes (Warton *et al.* 2006) fitted to log-transformed
166 data. The "static ratio" (LM:SM, LA:SM) and allometric (a_LMSM) descriptors were of
167 course correlated, but sufficiently weakly (mean r^2 across age/season datasets = 0.37) that
168 they contained substantial independent information about branch-scale leaf:stem allocation.

169 Stem tissue density (dry mass per fresh volume) was measured on 2 cm long branch
170 segments of approximately 1 cm over-bark diameter. For dry season samples, density was
171 measured on whole stems, including bark. For wet season samples, the bark was first
172 removed, allowing us to measure relative dry mass allocation to bark versus sapwood. For
173 these samples, stem density refers to that of the sapwood only (plus any pith, if present).
174 Hereafter we refer to these quantities as "WD" (wood density). At each date, five samples
175 were taken per species/age class. Sample volumes were measured using standard procedure
176 (via displacement), and dry masses after oven-drying at 70ºC for seven days.

177

178 *Growth rates*

179 The stem increment (growth rate) data were not measured as part of this study. Data for
180 northern Australian savanna species came from two sources: (1) The "Kapalga" dataset; and
181 (2) the "Three Parks" dataset (Murphy *et al.* 2010). Kapalga (12°50′S, 132°50′E) is located
182 200 km east of Darwin in Kakadu National Park. It was run as a CSIRO research station from
183 the mid-1970s to the mid-1990s. Various combinations of fire frequency and severity were
184 generated between 1990 and 1995 (Cook and Corbett 2003; Williams *et al.* 2003). Stem
185 diameters at 1.3 m height (DBH) were measured every 12 months. The "Three Parks" dataset
186 contains repeat-measured DBH data for savanna vegetation in Kakadu, Litchfield and
187 Nitmiluk National Parks (Northern Territory, Australia). At each of 163 locations, all
188 individuals with DBH ≥ 5 cm were initially measured between 1994 and 1997, then re-
189 measured twice, each time approximately five years apart. DBH measurements were made
190 during the wet season only (to avoid the stem shrinkage that may occur during dry
191 conditions). Fire severity and frequency was determined for each location/census period *post*
192 *hoc*, using survey data and aerial photographs (Murphy *et al.* 2010). Annual rainfall ranges
193 from 900 mm at Nitmiluk to 1470 mm at Kakadu (including Kapalga), with sites showing

194 similar seasonality (Murphy *et al.* 2010). Murphy et al (2010) – one of our two sources of
195 growth rate data – showed that DBH growth rate was unrelated to rainfall across this region,
196 suggesting that the GR data should be broadly representative of our study species, despite
197 Howard Springs receiving higher rainfall.

198 In savanna, fire damage to stems may result in very low or even negative stem
199 diameter increments between censuses. We took three steps to counter this issue. First, we
200 discarded all DBH data from sites designated as having experienced "severe" (Kapalga) or
201 "frequent, severe" (Three Parks) fire. Second, all negative increment data were discarded.
202 This resulted in a dataset with 7897 rows, each row describing a stem diameter increment for
203 some individual plant, for some census period. (Data from Kapalga contributed 5155 rows;
204 from Three Parks, 1340 rows from Kakadu NP, 765 from Litchfield NP, 637 from Nitmiluk
205 NP). Finally, we summarised the set of stem increment data for each species/age class using
206 80^{th} percentiles, rather than a measure of central tendency (Clark and Clark 1999; Rozendaal
207 *et al.* 2010; Wright *et al.* 2010). Doing so should minimise the influence of fire-damaged
208 plants and better facilitate quantifying trait-growth relationships of "successful" individuals
209 of each species and age class (by analogy, we measured traits such as photosynthetic rates on
210 recently-matured leaves which are near their peak physiological condition). There were too
211 few data to confidently estimate GR for saplings of *Acacia difficilis* and *Grevillea decurrens*,
212 meaning that we had GR data for 17 species as adults, and 15 species as saplings. Trait data
213 were averaged to give a single value for saplings and for adults, for each species, for each
214 sampling period (Table S1; Figs S1, S2). Almost all individuals of the two deciduous species
215 were leafless during dry season sampling, limiting analyses of GR-trait relationships for that
216 period to 16 species as adults and 13 species as saplings (Table 2).

217 In this study we were working across species with very different sizes at maturity.
218 Consequently we chose to use absolute rather than relative growth rate as our preferred

219 growth index, relative growth rate being strongly size-dependent (Iida *et al.* 2014; Rees *et al.*
220 2010), systematically decreasing with increasing plant size. By contrast, absolute growth
221 rates are generally relatively stable across broad ranges in plant size (Prior *et al.* 2006; Prior
222 *et al.* 2004).

223

224 *Analyses*

225 Ordinary least squares regression (including multiple regressions, with interaction terms) was
226 used to quantify relationships between GR and the various plant traits. For key bivariate
227 relationships we tested for heterogeneity among regression slopes fitted to each age-season
228 group. Where deemed non-heterogeneous (slope test, $P > 0.05$) a common slope can be fitted,
229 and whole-model explanatory power (r^2) and statistical significance can be reported. All
230 analyses were run in IBM SPSS Statistics v. 22, with the General Linear Model module used
231 for testing slope heterogeneity and calculating descriptors of common slopes.

232 An additional analysis specified by a reviewer and editor is reported in Supplementary
233 Appendix 1. There we report results from an analysis of phylogenetically independent
234 contrasts (PICs) calculated for GR in relation to key traits, for the wet season - adult data
235 subset only (this subset including all 17 species, and all traits including photosynthetic rates).

236

237 **RESULTS**

238 Sapling GR varied *ca*. 3-fold, from 0.37 cm yr^{-1} (*Corymbia bleeseri*) to 1.0 cm yr^{-1} (*Grevillea*
239 *pteridifolia*), median = 0.50 cm yr^{-1} (Table S1). Adult GR varied *ca*. 6-fold, from 0.25 cm yr^{-1}
240 (*Persoonia falcata*) to 1.56 cm yr^{-1} (*Acacia difficilis*, for which we lacked data for saplings),
241 median 0.42 cm yr^{-1}. Leaf-level traits (Table S1) varied 9-fold or less among species. By

242 contrast, leaf mass on terminal branches varied 16-fold among species, wood mass 34-fold,
243 and their ratio, 17-fold.

244

245 *Growth Rate – leaf trait relationships*

246 SLA was unrelated to GR in any of the four comparisons (two age classes, two sampling
247 periods; all $r^2 \leq 0.03$, $P > 0.4$; Fig. 1a, Table 2). Leaf N and P, expressed either per mass or
248 per area, were also unrelated to GR in every case (all $r^2 \leq 0.15$, with most $r^2 \leq 0.07$, and all P
249 > 0.14; Table 2). By contrast, A_{sat} explained a substantial proportion of growth rate variation
250 in adults ($r^2 = 0.32$; $P = 0.017$) as well as saplings ($r^2 = 0.23$; $P = 0.071$; Fig. 1b). The
251 common fitted slope of $\log_{10}$GR on $\log_{10}A_{sat}$ was 1.0 (whole-model $r^2 = 0.31$), indicating
252 direct proportionality: on average, a two-fold increase in A_{sat} corresponded to a two-fold
253 increase in stem diameter growth rate.

254 Variation in A_{sat} can be underpinned by variation in stomatal conductance to water
255 (g_s) and by the extent of CO_2 drawdown during photosynthesis, indexed here via leaf $\delta^{13}C$.
256 The observed GR – A_{sat} relationships were seemingly underpinned more by variation in g_s
257 than by CO_2 drawdown, g_s being more consistently related to GR than was $\delta^{13}C$ (Table 2),
258 and relationships between A_{sat} and g_s being tighter than those between A_{sat} and $\delta^{13}C$ ($r^2 =$
259 0.63 – 0.70 *vs*. 0.25 – 0.35, respectively).

260

261 *Growth Rate – stem trait relationships*

262 Growth rate was unrelated to either sapwood or whole-stem tissue density (Fig. 2a; Table 2).
263 Fractional bark allocation varied from *ca.* 20 % to 60 % by mass and was unrelated to GR in
264 saplings, and negatively correlated with GR among adults ($r^2 = 0.30$, $P = 0.024$; Fig 2b). That

said, the sapling and adult slopes were deemed not significantly different from one another (slope test, $P = 0.223$), with the common fitted slope significantly negative ($P = 0.016$; model $r^2 = 0.21$). This suggests some tendency for species with higher relative investment in bark to have slower stem diameter growth rates.

Relationships between GR and branch-scale biomass allocation

Total leaf mass was unrelated to GR in each of the four comparisons (Fig 3a; all $P > 0.1$). For adult plants, stem mass was negatively related to growth rate ($r^2 = 0.27 – 0.32$; Fig. 3b); for saplings, no relationship was observed (Table 2). Nonetheless, the four stem mass – GR slopes did not differ significantly from one another ($P = 0.731$), with the common slope explaining 25% of GR variation (significantly negative, $P < 0.001$).

Leaf and stem mass tended to explain more variation in growth rate when considered together, rather than one at a time. LM:SM explained between 16 % and 65 % variation in GR, depending on plant age and season (Fig. 3c). The four GR – LM:SM regression slopes were deemed non-heterogeneous ($P = 0.414$), with the common fitted slope explaining 33% variation in GR (significantly positive slope, $P < 0.001$). The allometric descriptor a_LMSM explained between 32 % and 51% variation in GR (Fig. 3d; Table 2). The four GR – a_LMSM regressions were deemed non-heterogeneous ($P = 0.300$), with a common fitted slope explaining 36% variation (significantly positive slope, $P < 0.001$).

Combined explanatory power of leaf:stem allocation and photosynthesis

To be consistent with treating photosynthetic rate (A_{sat}) on a per area basis, for this analysis we used the ratio of leaf *area* to stem mass (LA:SM), rather than LM:SM. Regression models

288 including an interaction term between A_{sat} and LA:SM were run first. With these interactions
289 deemed non-significant for both saplings and adults (both $P > 0.2$), we next ran models
290 including main effects only. For adults, A_{sat} and LA:SM together explained 64 % of GR
291 variation, with each variable contributing similar explanatory power (as judged by their
292 respective F-statistics; Table 3). For saplings, the two traits explained 28 % of GR variation,
293 just a modest improvement over A_{sat} on its own ($r^2 = 0.23$; Table 2), and in this case the
294 coefficient for LA:SM was non-significant and that for A_{sat} just marginally so (Table 3).

295 For the allometric descriptor we continued to use a_LMSM (the mass-basis
296 allometry). For adults, A_{sat} and a_LMSM explained 80% of GR variation, in a regression
297 model that included a highly significant, positive interaction between the traits (Table 3).
298 This interaction term indicated that the effect of higher A_{sat} on GR was stronger in species
299 with higher a_LMSM, and vice versa. For saplings, the two traits explained 41% of GR
300 variation (Table 3), just a modest improvement of a_LMSM on its own ($r^2 = 0.32$; Table 2),
301 and in this case the coefficient for A_{sat} was non-significant (Table 3).

302 For the adult dataset these relationships were strongly influenced by *Acacia difficilis*.
303 Re-running the analyses with this species removed, A_{sat} and a_LMSM together still explained
304 57% of GR variation (multiple regression with interaction term; not shown), and A_{sat} and
305 LA:SM explained 34 % (main effects only; not shown).

306 A supplementary analysis, incorporating phylogenetic information as
307 Phylogenetically Independent Contrasts (Supplementary Appendix 1), gave additional
308 strength to our results. In those analyses also, variation in growth rate was clearly
309 (significantly) connected to variation in leaf:stem allometry, A_{sat} and fractional bark
310 allocation, but not to variation in either SLA or wood density.

311

DISCUSSION

Photosynthetic rate as a driver of GR variation

Light-saturated photosynthetic rate, A_{sat}, explained roughly 30% of interspecific variation in stem diameter growth rates. This mirrors the generally positive A_{sat} – growth rate relationship known from controlled-environment seedling studies (Kruger and Volin 2006) and older seedlings grown for two years in a shade house (Li *et al.* 2016). By contrast, there have been rather few field-based tests of GR – A_{sat} relationships, especially for sapling or adult plants. A positive relationship has been reported across several vegetation types in northern Australia (Prior *et al.* 2004), from open forest in Hawaii (Stratton and Goldstein 2001), and from saplings of 53 species growing in high-light gaps within a Bolivian rainforest (Poorter and Bongers 2006). No relationship was observed among 24 savanna and forest species in Brazil (Rossatto *et al.* 2009).

A generally positive GR – A_{sat} relationship makes intuitive sense, especially in high light situations. That said, species with higher A_{sat} could in principle deploy less total leaf area, or have higher leaf replacement costs (shorter leaf lifespan), or have higher belowground or sapwood respiration costs, and these costs could potentially cancel out the growth benefit of higher A_{sat}. However, for both adults and saplings of the 17 species examined here this was seemingly not the case, in support of the prediction that the GR – A_{sat} relationship does not vary with plant stature (Gibert *et al.* 2016).

Leaf:stem allocation as a driver of GR variation

This study represents the first test of the proposition that higher relative allocation to leaf versus stems, considered at branch level, should drive faster growth at the whole-plant level

335 (Pickup *et al.* 2005). Those authors argued that higher allocation to leaf represented greater
336 potential for photosynthetic benefits, while higher allocation to stem would incur higher costs
337 for maintenance respiration. All else equal, a more positive carbon balance at branch-level
338 should lead to more carbon exported to other parts of the plant, and thus faster growth
339 (Pickup *et al.* 2005). Our results are consistent with this interpretation. However, as it turned
340 out, the positive influence of leaf:stem allocation on growth rate was more strongly driven by
341 stem allocation (which was negatively correlated with GR) than by leaf mass (which was
342 unrelated to GR).

343 Higher investment in stem tissues must also have benefits, for example it may
344 represent more biomechanical support and hydraulic supply to leaves, greater potential for
345 water storage in sapwood and the living inner bark layers (Rosell 2016), and greater
346 protection against fire, especially from the outer bark layers (Pausas 2014). Presumably, all of
347 these features can be important in seasonally-dry, frequently-burnt savannas, such as that
348 studied here.

349

350 *No general relationship between GR and SLA for field-grown plants*

351 The other key finding from this study is the null result, that SLA failed to explain variation in
352 GR for either saplings or adult plants. The size-dependence of GR – SLA relationships has
353 been investigated in several recent studies, but conclusions have varied. SLA and stem
354 diameter growth rate were: positively correlated among Puerto Rico rainforest species, with
355 no size-related trend in relationship strength (Lasky *et al.* 2015); unrelated across all size
356 classes in a very detailed study of Panamanian rainforest species (Visser *et al.* 2016);
357 unrelated across all size classes except mid-size trees (DBH = 16-18 cm) in a seasonally dry
358 forest, Brazil (Prado-Junior *et al.* 2016); and positively correlated among adult rainforest

359 trees in Taiwan, but *negatively* correlated among juveniles (Iida *et al.* 2014). Mostly these
360 studies have focused on forests with a marked vertical light gradient and (at least partially as
361 a result) marked shifts in leaf traits between young and old plants. Our study represents an
362 important contrast, coming from open vegetation with little vertical light gradient, and where
363 leaf and wood traits of saplings were indistinguishable from adults (Fig. S1).

364

365 *GR unrelated to stem tissue density and leaf nutrient concentrations*

366 Other hypotheses detailed in the Introduction receiving no support were the predictions that
367 GR would be negatively related to WD, and positively related to leaf N and P concentrations.
368 A negative relationship between stem diameter growth rates and trunk wood density has been
369 reported many times (Iida *et al.* 2014; King *et al.* 2006; Lasky *et al.* 2015; Martínez-Vilalta *et*
370 *al.* 2010; Poorter *et al.* 2008; Wright *et al.* 2010), although null relationships have also been
371 reported (Russo et al. 2010). Even when statistically significant the explanatory power is
372 generally rather low in these studies, typically < 10% (but see Martínez-Vilalta *et al*. 2010),
373 and sample size (number of species) is usually far higher than used here. Perhaps we lacked
374 sufficient power to detect a relationship between growth rate and wood density, if indeed
375 there is a general tendency for this to be true among Australian savanna species. Here we
376 measured tissue density on terminal branches rather than main trunks; however, these
377 properties would likely be related (Swenson and Enquist 2008), and their relationships to GR
378 therefore similar.

379 Growth rates were also unrelated to leaf N and P concentrations (considered per unit
380 leaf area or mass). Perhaps this should not be surprising since A_{sat} was at best marginally
381 correlated with N_{area} (in saplings, $r = 0.46$, $P = 0.062$) and unrelated to P_{area} in both age
382 groups ($P > 0.140$; not shown), and the causal pathway between leaf N (and P) and GR

arguably flows via their respective links to photosynthesis. Considered on a leaf mass basis, leaf N, leaf P and photosynthetic rate were all correlated with SLA (not shown). Covariation in this suite of traits can be thought of representing variation along a "leaf economic spectrum" (Wright *et al.* 2004). Hence, the finding that all of SLA, N_{mass} and P_{mass} were unrelated to GR (Table 2) can also be taken to illustrate how strategy variation along the leaf economic spectrum does not necessarily map on to variation in growth rate of field-grown plants.

Successful growth – trait strategies

Our results help us understand the biology underpinning differences among species in their growth rates. For example, the short-lived, fire-sensitive species *A. difficilis* was the fastest growing species, with this high GR seemingly driven by the combination of high leaf:stem mass ratio (1.6 - 2.9 $g.g^{-1}$ depending on season; Table S1), low fractional allocation to bark (23 %) and fast A_{sat} (26 μmol m^{-2} s^{-1}), itself associated with profligate photosynthetic water use (g_s; 1087 mmol m^{-2} s^{-1}). *Grevillea pteridifolia* seemingly achieves its fast GR by teaming high LM:SM (*ca.* 3.6 g g^{-1} in saplings, 2.4 g g^{-1} in adults) with medium-high A_{sat} (18.2 – 19.7 μmol m^{-2} s^{-1}), while *Eucalyptus miniata* does so by teaming very rapid A_{sat} (*ca.* 25 μmol m^{-2} s^{-1}) with mid-range LM:SM (1.2 – 1.7 $g.g^{-1}$). Conversely, the slow GR of adult *Petalostigma pubescens* was associated with the lowest mean A_{sat} value (12.4 μmol m^{-2} s^{-1}), slow g_s (392 mmol m^{-2} s^{-1}) and low LM:SM (*ca.* 1.0 g g^{-1}). The slow GR of sapling *Buchanania obovata* was associated with the lowest A_{sat} values (11.6 μmol m^{-2} s^{-1}) seen for saplings, the lowest g_s (301 mmol m^{-2} s^{-1}), low LM:SM (0.6 – 0.9 g g^{-1}, depending on season), and the highest fractional allocation to bark (60%).

That these species vary widely in stem diameter growth rate yet still co-occur indicates that there are many equally successful growth and survival strategies in this system. Of particular importance, not addressed in this study, is the need for sufficient individuals of each species to overcome the demographic bottleneck that frequent, intense fires create – the so-called sapling "fire trap" (Bond 2008; Prior *et al.* 2010). For investigating that aspect of the growth strategy, additional data for height growth rate would be especially valuable.

Synthesis

Our results suggest that branch-level biomass allocation is a property deserving serious attention in future studies of plant growth. Here we presented two types of indices: static ratios (LM:SM, LA:SM), and an allometric descriptor (a_LMSM). Not surprisingly a_LMSM and LM:SM were correlated, but weakly enough that each variable contains considerable independent information. Besides explaining considerable variation in GR, branch-level biomass allocation also has the virtue of being easy to measure.

Together, A_{sat} and leaf:stem deployment explained up to 41% GR variation in saplings and up to 80% in adults (57% with *Acacia difficilis* excluded). These results are remarkable given that we did not consider interspecific variation in, for example, canopy architecture, below-ground allocation, or tissue turnover rates. Of course, the extent to which these results generalise to other savannas or other vegetation types will require further study. On the face of it, one might predict lower explanatory power for these traits in vegetation types where many individuals are shaded, or where many individuals are very large (i.e., situations where the benefits of higher A_{sat} are likely muted, and where sapwood respiration costs begin to dominate GR variation). Testing this hypothesis would be a useful next step.

Currently we lack clear demonstration (i.e., within a single empirical study) that SLA – growth rate relationships flip as predicted, from positive in small plants to null in large plants. Nonetheless we suggest that this is likely the case, given the wealth of seedling studies showing strong positive relationships and the increasing number of sapling-adult studies showing little if any relationship. Even so, it is as yet unclear at what plant size these shifts occur and whether they occur systematically earlier or later in particular light environments or vegetation types, or in plants with particular architectures or growth strategies.

That SLA is often unrelated to growth rates of field-grown plants has been disappointing for authors expecting plant functional traits to neatly explain demographic variation (Paine *et al.* 2015; Wright *et al.* 2010). Nonetheless, SLA remains a key trait for understanding leaf economic variation (Westoby *et al.* 2002); a key descriptor of how canopy mass interconverts with canopy light-capturing area (and thus an important property in plant growth models); and it is related to important ecological variation at other scales – for example, herbivory rates, flammability, and litter decomposition rate (Poorter *et al.* 2009). But, it seems increasingly clear that SLA and plant growth rate are generally correlated only in very small plants, and this fact should be more widely appreciated.

Author contributions

IJW and CEL designed the study. All authors contributed to fieldwork and discussion of results. IJW analysed the data and drafted the manuscript. All authors contributed to subsequent versions.

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630

Table 1. List of study species, some key life history characteristics, the stem diameter cut-offs (at 1.3 m height) used to distinguish small plants ("saplings") from large plants ("adults"), and the sample size (number of data points) used for estimating stem-diameter growth rates. Semi-deciduous species are evergreen, but exhibit a noticeable thinning of the canopy during the dry season.

Species	**Family**	**Leaf phenology**	**Habit**	**N_2 fixer**	**DBH cut-off (cm)**	**GR sample size (saplings, adults)**
Acacia difficilis	Fabaceae	Evergreen	Shrub	Yes	1.5	- , 19
Acacia latescens	Fabaceae	Evergreen	Shrub	Yes	3	77, 67
Acacia mimula	Fabaceae	Evergreen	Shrub	Yes	3	15, 31
Buchanania obovata	Anacardiaceae	Semi-deciduous	Tree	No	6	31, 95
Cochlospermum fraseri	Bixaceae	Deciduous	Tree	No	3	8, 21
Corymbia bleeseri	Myrtaceae	Semi-deciduous	Tree	No	6	44, 220
Corymbia porrecta	Myrtaceae	Semi-deciduous	Tree	No	6	207, 752
Erythrophleum chlorostachys	Fabaceae	Semi-deciduous	Tree	Yes	6	273, 741
Eucalyptus miniata	Myrtaceae	Evergreen	Tree	No	6	635, 1559
Eucalyptus tetrodonta	Myrtaceae	Evergreen	Tree	No	6	346, 1810
Grevillea decurrens	Proteaceae	Semi-deciduous	Shrub	No	3	- , 9
Grevillea pteridifolia	Proteaceae	Semi-deciduous	Shrub	No	3	12, 94
Lophostemon lactifluus	Myrtaceae	Semi-deciduous	Tree	No	6	34, 159
Persoonia falcata	Proteaceae	Semi-deciduous	Shrub	No	3	4, 36
Petalostigma pubescens	Picrodendraceae	Evergreen	Tree	No	6	24, 48
Planchonia careya	Lecythidaceae	Deciduous	Tree	No	3	4, 147
Xanthostemon paradoxus	Myrtaceae	Semi-deciduous	Tree	No	6	207, 168

Table 2. Tests for correlation between stem-diameter growth rates and various plant functional traits for the four age-season datasets. Correlations at least marginally significant ($P < 0.1$) are shown in bold, and the sign of these relationship is also indicated.

Trait abbreviations. SLA: specific leaf area; N_{mass}, N_{area}: leaf N per mass and area; P_{mass}, P_{area}: leaf P per mass and area; A_{sat}: light-saturated photosynthetic rate; g_s: stomatal diffusional conductance to water; LM: leaf mass; SM: stem mass; LA: leaf area; a_LM/SM: allometric slope describing leaf mass allocation relative to stem mass allocation. Note, "wood density" refers to whole-stem tissue density for dry season sampling, and density of sapwood only for the wet season.

Trait	**Saplings (dry season)**	**Saplings (wet season)**	**Adults (dry season)**	**Adults (wet season)**
	r^2, P, n, sign	r^2, P, n, sign	r^2, P, n, sign	r^2, P, n, sign
log SLA ($cm^2\ g^{-1}$)	0.02, 0.664, 13	0.002, 0.870, 15	0.02, 0.633, 16	0.03, 0.492, 17
log N_{mass} (%)	0.06, 0.425, 13	0.03, 0.536, 15	0.04, 0.499, 15	0.13, 0.149, 17
log N_{area} ($g\ m^{-2}$)	0.05, 0.468, 13	0.05, 0.409, 15	0.08, 0.315, 15	0.07, 0.302, 17
log P_{mass} (%)	0.15, 0.193, 13	0.11, 0.226, 15	0.02, 0.606, 15	0.05, 0.397, 17
log P_{area} ($g\ m^{-2}$)	0.04, 0.526, 13	0.11, 0.223, 15	0.04, 0.487, 15	<0.001, 0.997, 17
log A_{sat} ($\mu mol\ m^{-2}\ s^{-1}$)		**0.23, 0.071, 15,** +		**0.32, 0.017, 17,** +
log g_s ($mmol\ m^{-2}\ s^{-1}$)		**0.20, 0.095, 15,** +		**0.17, 0.095, 17,** +
Leaf $d^{13}C$ (‰)	0.03, 0.59, 12	**0.25, 0.056, 15, -**	0.01, 0.736, 16	0.13, 0.157, 17
log LM (g)	0.22, 0.101, 13	0.03, 0.520, 15	0.02, 0.613, 16	0.09, 0.252, 17
log SM (g)	0.13, 0.225, 13	0.09, 0.290, 15	**0.27, 0.039, 16, -**	**0.32, 0.019, 17, -**
log LM:SM ($g\ g^{-1}$)	**0.65, 0.001, 13,** +	0.16, 0.134, 15	**0.18, 0.097, 16,** +	**0.44, 0.004, 17,** +
a_LM/SM	**0.51, 0.006, 13,** +	**0.32, 0.027, 15,** +	**0.41, 0.008, 16,** +	**0.32, 0.017, 17,** +
log LA:SM ($cm^2\ g^{-1}$)	**0.66, 0.001, 13,** +	0.08, 0.313, 15	0.15, 0.132, 16, +	**0.35, 0.013, 17,** +
Bark % mass		0.05, 0.443, 15		**0.30, 0.024, 17, -**
Wood density ($g\ cm^{-3}$)	0.002, 0.896, 13	<0.001, 0.947, 15	0.001, 0.923, 15	0.03, 0.473, 17

Table 3. Multiple regressions exploring the interactive effects of photosynthetic rate and leaf:stem allocation on plant growth rates

GR ~ A_{sat}, LA:SM (interaction was never significant)			
ADULTS (r^2 = 0.64, P < 0.001, df = 16)			
Variable	**F**	**Coefficients**	**P**
Intercept	29.83	-2.53 (-3.52, -1.54)	<0.001
log A_{sat}	11.29	1.12 (0.41, 1.84)	0.005
log LA:SM	12.25	0.41 (0.16, 0.66)	0.004
SAPLINGS (r^2 = 0.28, P = 0.022, df = 14)			
Variable	**F**	**Coefficients**	**P**
Intercept	6.945	-1.43 (-2.61, -0.25)	0.022
log A_{sat}	3.261	0.75 (-0.16, 1.66)	0.096
log LA:SM	0.766	0.10 (-0.15, 0.35)	0.399
GR ~ A_{sat}, a_LMSM, A_{sat} × a_LMSM (where significant)			
ADULTS (model r^2 = 0.80, p < 0.001, df = 16)			
Variable	**F**	**Coefficients**	**P**
Intercept	13.36	6.27 (2.56, 9.98)	0.003
log A_{sat}	16.45	-5.76 (-8.84, -2.69)	0.001
a_LMSM	20.22	-9.64 (-14.27, -5.01)	0.001
log A_{sat} × a_LMSM	22.44	8.34 (4.54, 12.14)	<0.001
SAPLINGS (model r^2 = 0.41, P = 0.042, df = 14)			
Variable	**F**	**Coefficients**	**P**
Intercept	5.86	-1.15 (-2.18, -0.12)	0.032
log A_{sat}	1.78	0.53 (-0.34, 1.4)	0.207
a_LM:SM	3.69	0.26 (-0.03, 0.55)	0.079

FIGURE CAPTIONS

Figure 1. Relationships between stem diameter growth rate and (a) specific leaf area, SLA; and (b) Light-saturated photosynthetic assimilation rate, A_{sat}, for each of the age-season datasets (note, photosynthesis measurements were made during the wet season only). Each data point represents a different species. Significant regression slopes ($P < 0.05$) shown as solid lines; marginally significant slopes ($0.05 < P < 0.10$) with dashed lines (full details given in Table 2). Symbols. Pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season.

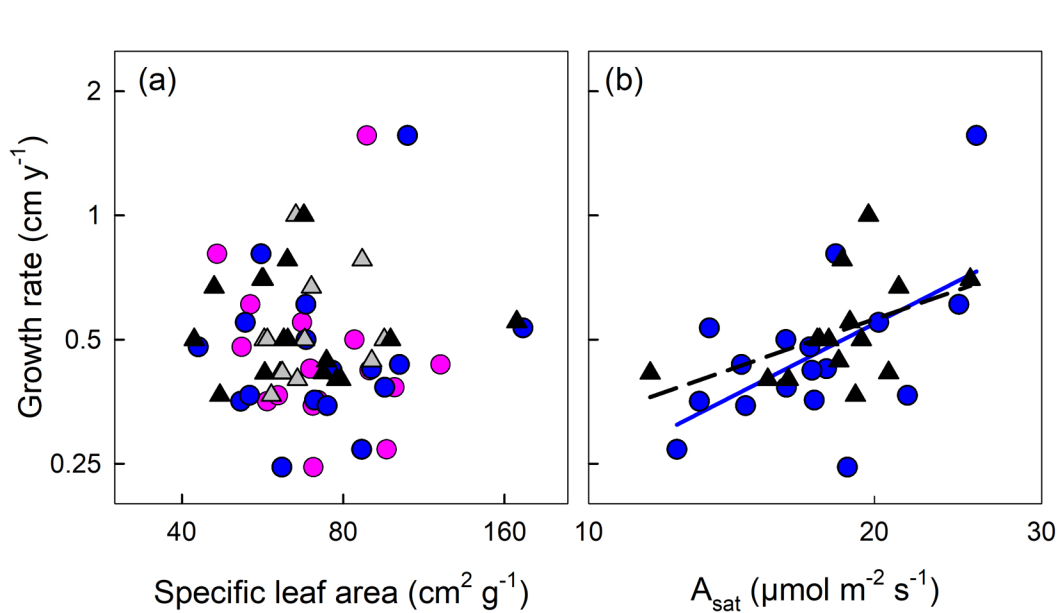
Figure 2. Relationship between stem diameter growth rate and properties of 1 cm diameter terminal stems. (a) Whole-stem (dry season) or sapwood (wet season) tissue density. (b) Percentage of stem mass allocated to bark (wet season only). Solid regression line indicates the relationship was significant ($P < 0.05$); see Table 2. Symbols. Pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season.

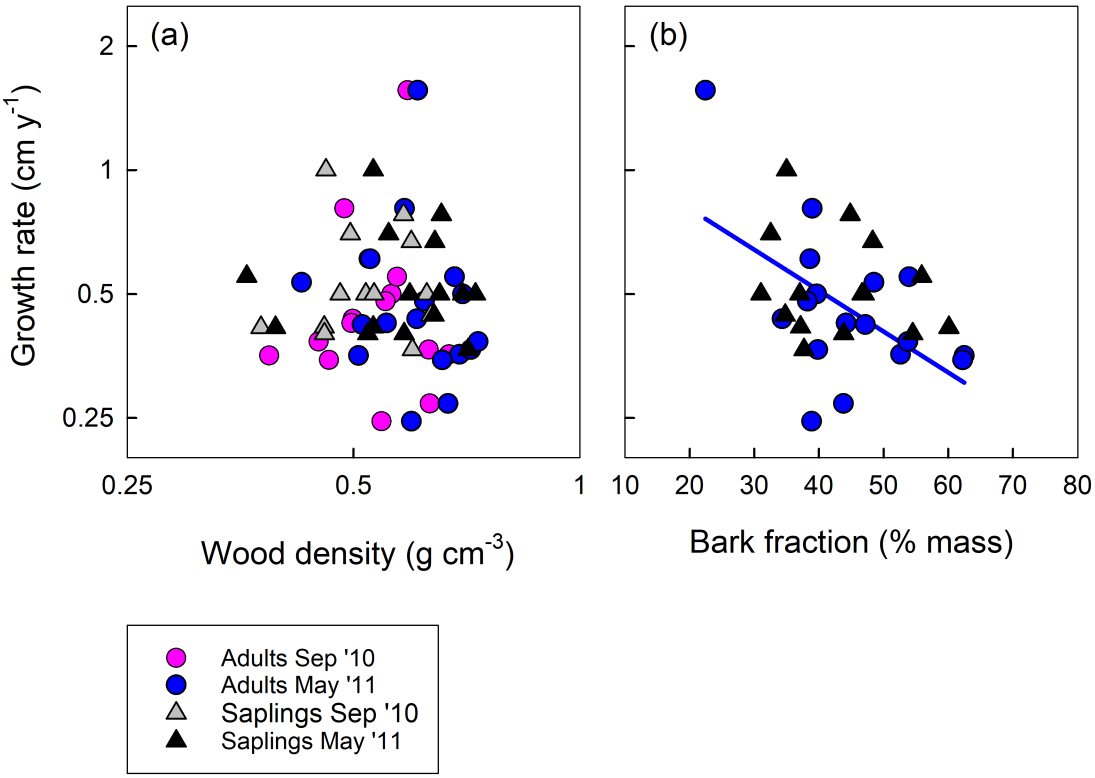
Figure 3. Relationship between stem diameter growth rate and leaf versus stem deployment on terminal branches. (a) Total leaf mass; (b) Total stem mass (including bark); (c) Ratio of leaf:stem mass. (d) Allometric coefficient describing the rate of leaf mass accumulation versus stem mass accumulation along the branch. Significant regression slopes ($P < 0.05$) shown as solid lines; marginally significant slopes ($0.05 < P < 0.10$) with dashed lines (full details given in Table 2). Symbols. Pink circles: adults, dry season; blue circles: adults, wet season; grey triangles: saplings, dry season; black triangles: saplings, wet season.

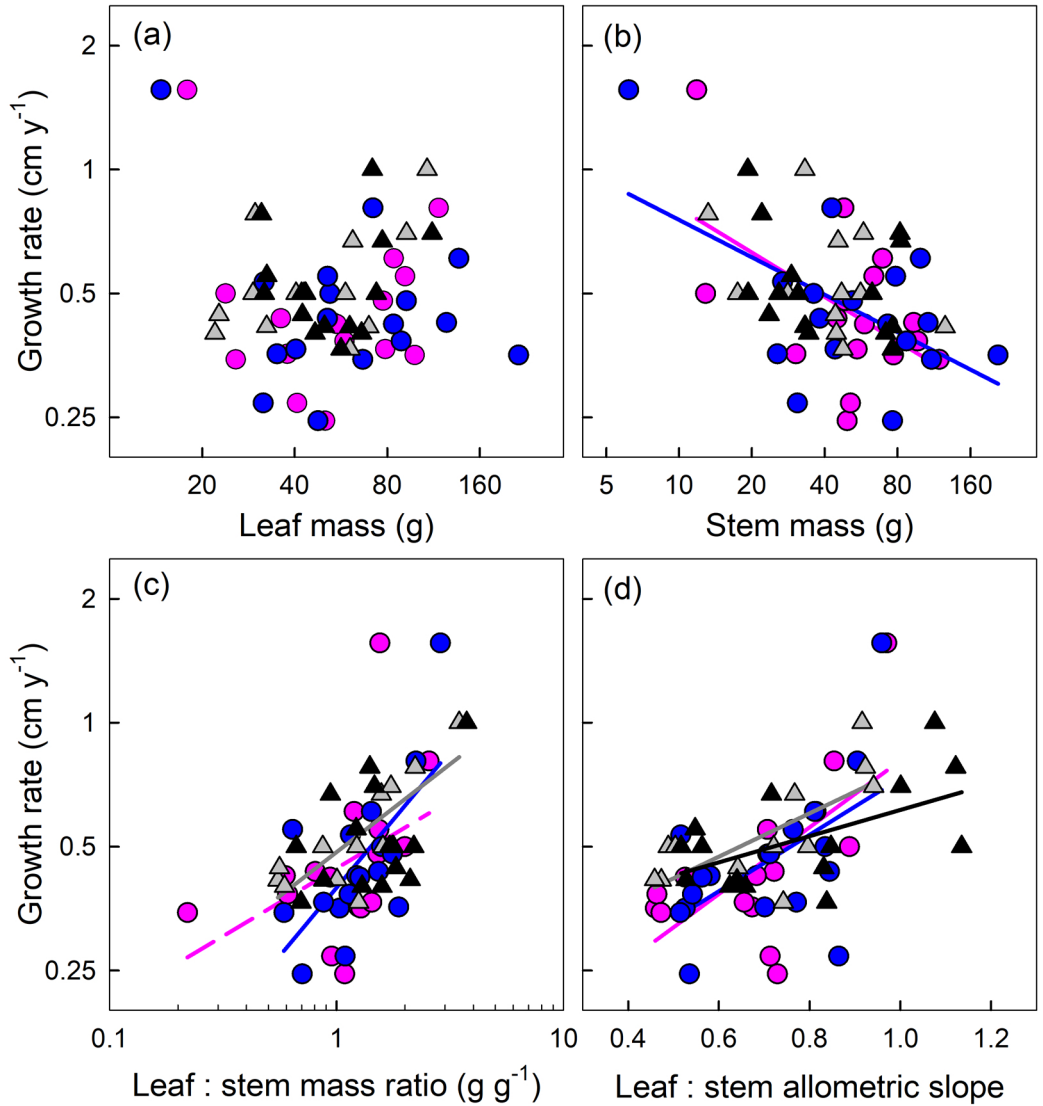
Figure S1. Comparison of growth rate and trait values of adults and saplings for each of the study species (Table 1). For trait data each data point represents the mean of *ca.* five replicates (see Methods). In each panel the 1:1 line is shown in black. There were insufficient

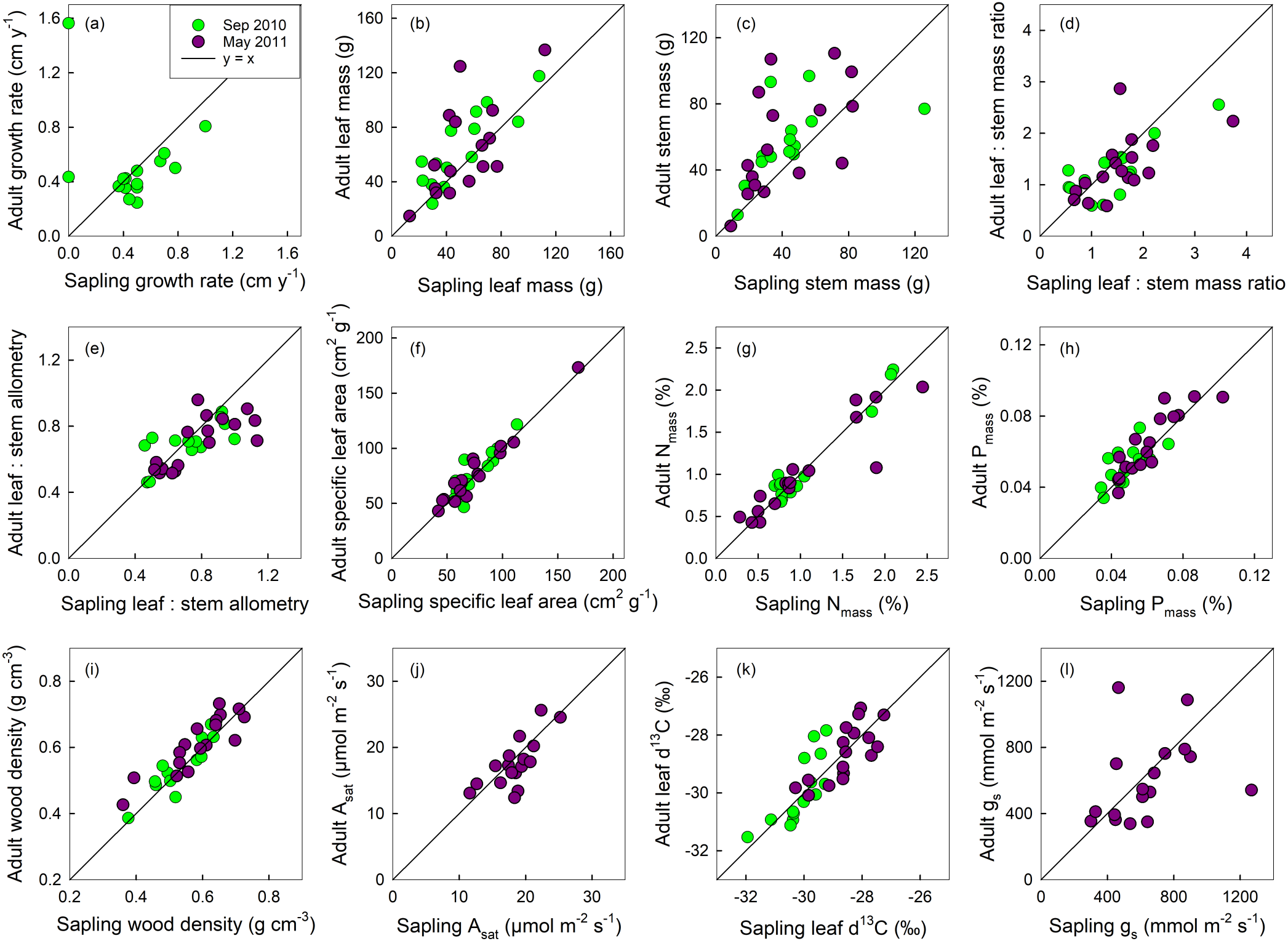
data to calculate growth rates for saplings of *Acacia difficilis* and *Grevillea decurrens*, so in panel (a) these are shown with GR = 0. September 2010 = dry season; May 2011 = wet season.

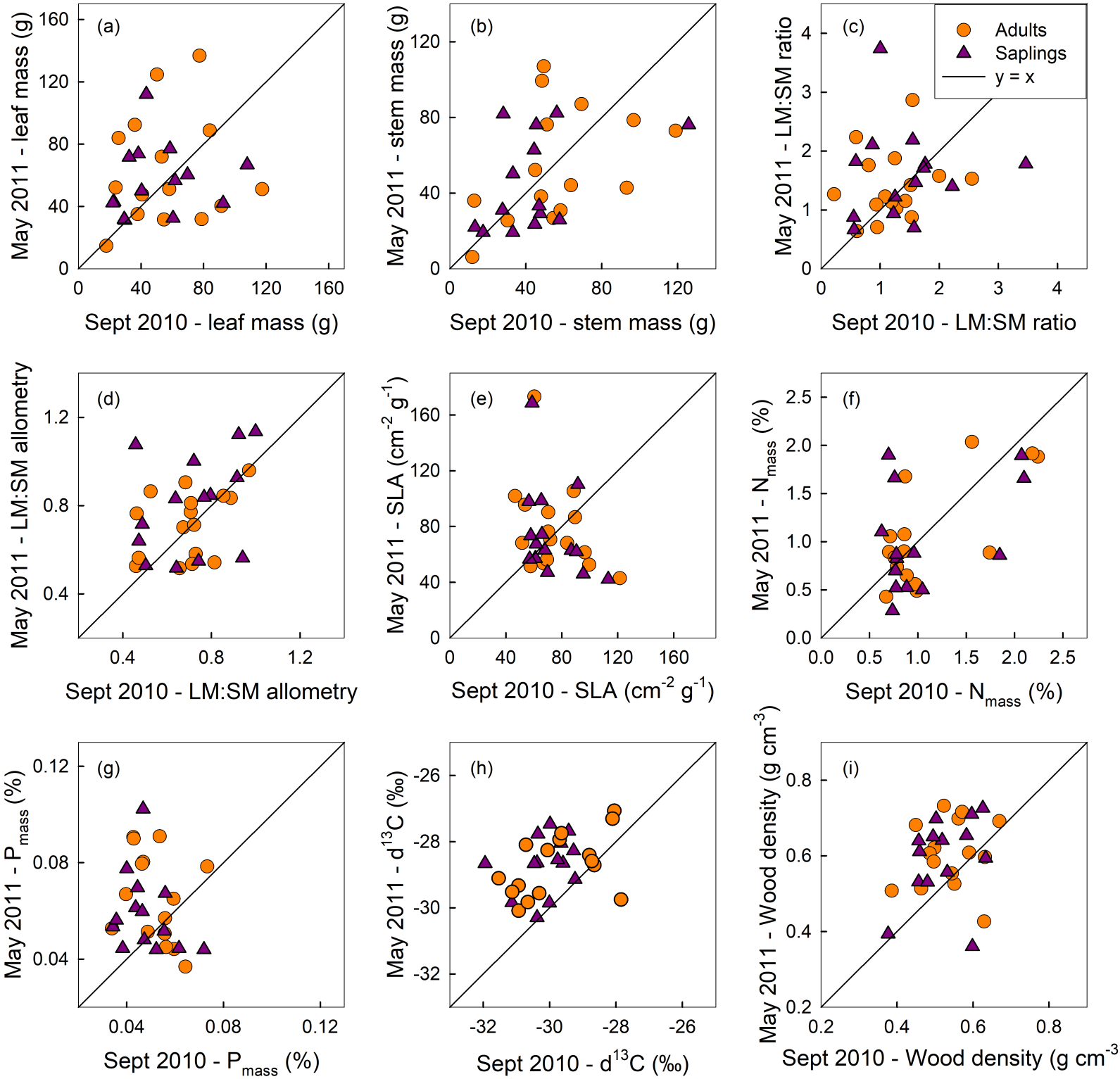
Figure S2: Comparison of trait values between the two seasons sampled (wet season, May 2011; dry season September 2010) for both adults (orange circles) and saplings (purple triangles) of 17 species. Points represent species-mean values calculated from *ca*. five individual plants (see Methods). In each panel the 1:1 line is shown in black. 'Wood' density measurements in 2010 (dry season) included bark and sapwood. Repeating this in 2011 (wet season) we removed the bark, giving the density of sapwood only (and in most cases higher values).


(a)
(b)
Growth rate (cm y-1)
2
1
0.5
0.25
40
80
160
10
20
30
Specific leaf area (cm2 g-1)
Asat (μmol m-2 s-1)

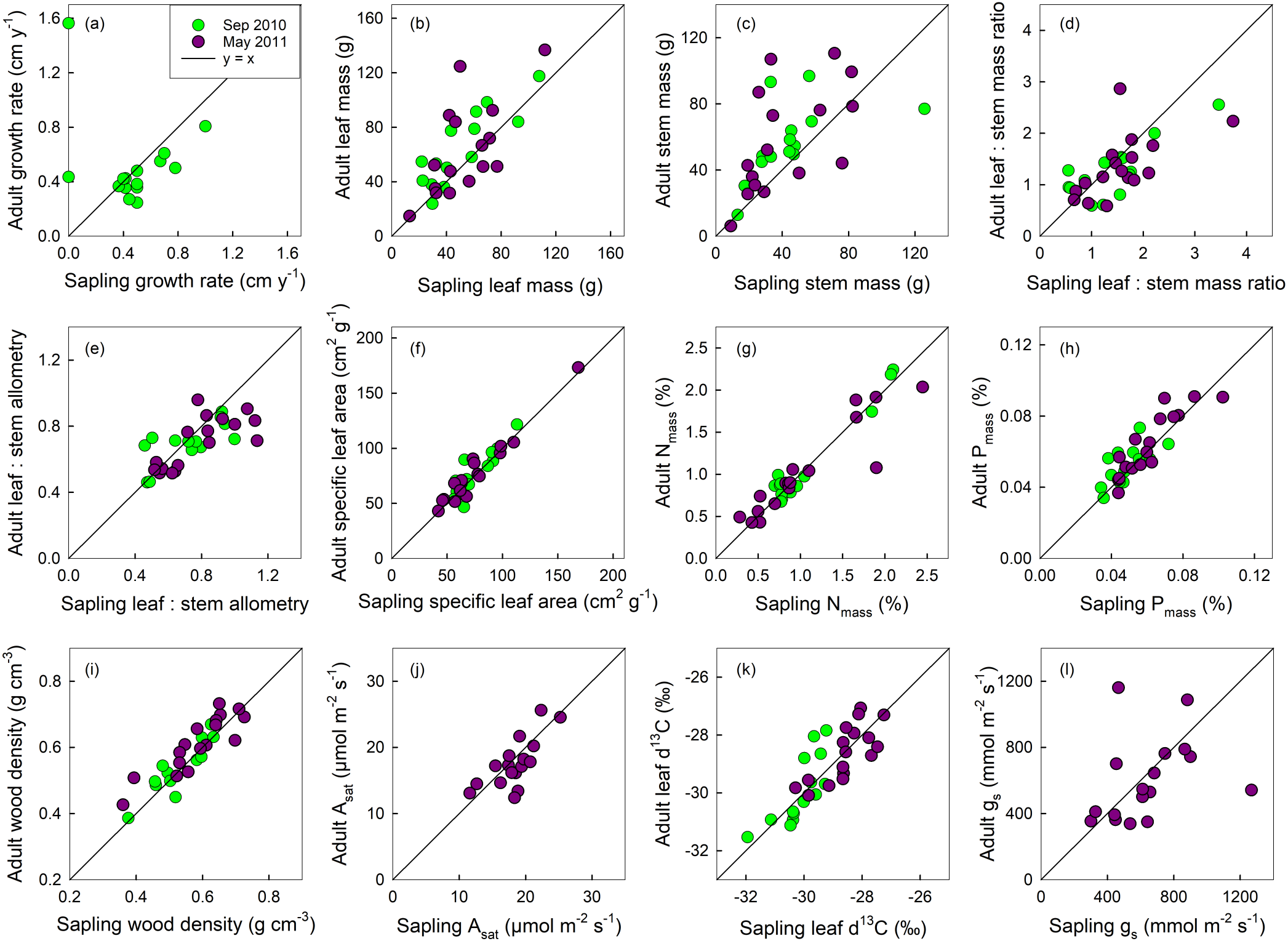

(a)
(b)
Growth rate (cm y-1)
2
1
0.5
0.25
0.25
0.5
1
10
20
30
40
50
60
70
80
Wood density (g cm-3)
Bark fraction (% mass)
Adults Sep '10
Adults May '11
Saplings Sep '10
Saplings May '11


(a)
(b)
(c)
(d)
Growth rate (cm y-1)
2
1
0.5
0.25
20
40
80
160
Leaf mass (g)
5
10
20
40
80
160
Stem mass (g)
0.1
1
10
Leaf : stem mass ratio (g g-1)
0.4
0.6
0.8
1.0
1.2
Leaf : stem allometric slope

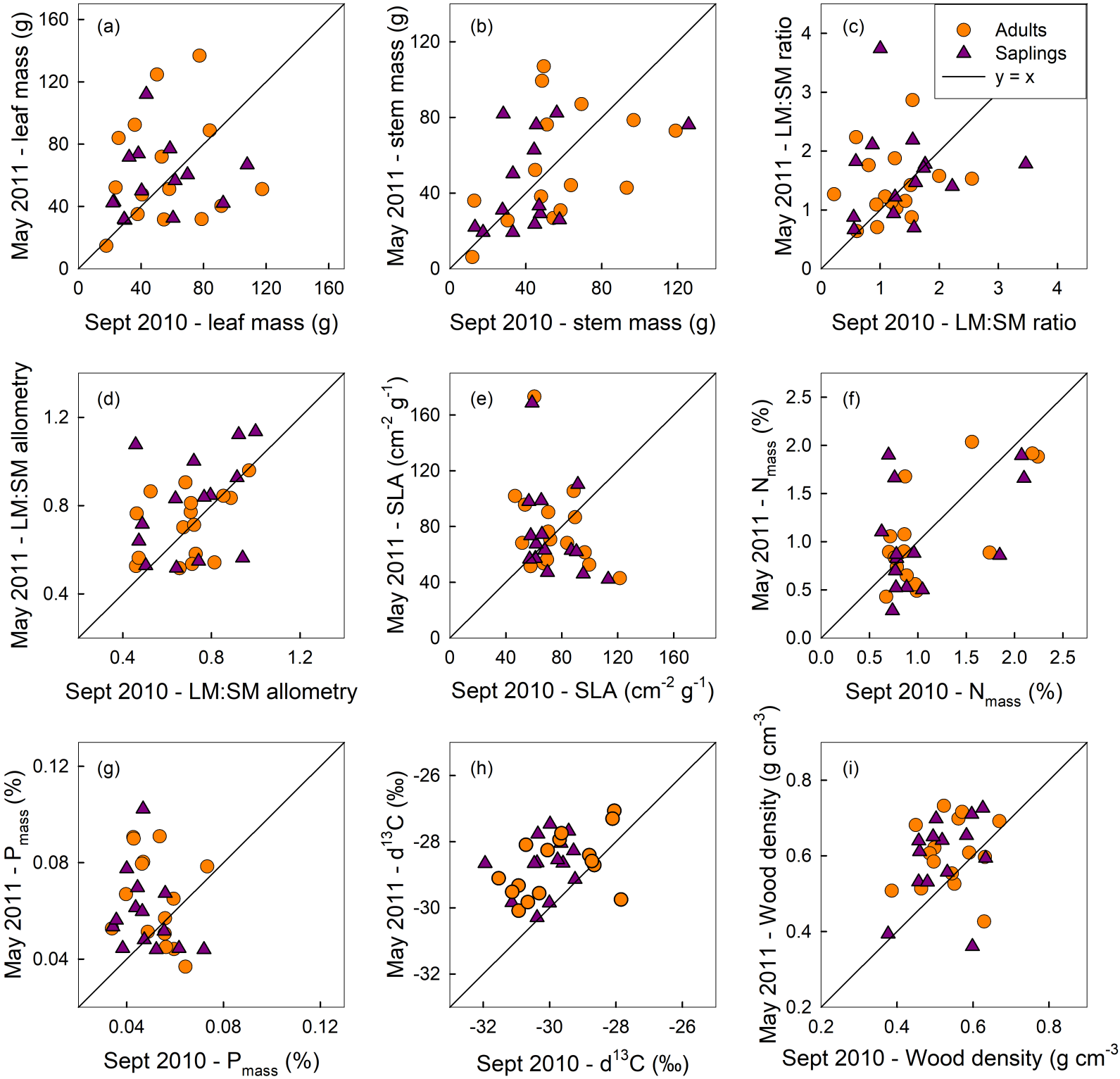

(a)
Sep 2010
May 2011
y = x
Adult growth rate (cm y-1)
Sapling growth rate (cm y-1)
(b)
Adult leaf mass (g)
Sapling leaf mass (g)
(c)
Adult stem mass (g)
Sapling stem mass (g)
(d)
Adult leaf : stem mass ratio
Sapling leaf : stem mass ratio
(e)
Adult leaf : stem allometry
Sapling leaf : stem allometry
(f)
Adult specific leaf area (cm2 g-1)
Sapling specific leaf area (cm2 g-1)
(g)
Adult Nmass (%)
Sapling Nmass (%)
(h)
Adult Pmass (%)
Sapling Pmass (%)
(i)
Adult wood density (g cm-3)
Sapling wood density (g cm-3)
(j)
Adult Asat (μmol m-2 s-1)
Sapling Asat (μmol m-2 s-1)
(k)
Adult leaf d13C (‰)
Sapling leaf d13C (‰)
(l)
Adult gs (mmol m-2 s-1)
Sapling gs (mmol m-2 s-1)


(a)
May 2011 - leaf mass (g)
Sept 2010 - leaf mass (g)
(b)
May 2011 - stem mass (g)
Sept 2010 - stem mass (g)
(c)
Adults
Saplings
y = x
May 2011 - LM:SM ratio
Sept 2010 - LM:SM ratio
(d)
May 2011 - LM:SM allometry
Sept 2010 - LM:SM allometry
(e)
May 2011 - SLA (cm-2 g-1)
Sept 2010 - SLA (cm-2 g-1)
(f)
May 2011 - Nmass (%)
Sept 2010 - Nmass (%)
(g)
May 2011 - Pmass (%)
Sept 2010 - Pmass (%)
(h)
May 2011 - d13C (‰)
Sept 2010 - d13C (‰)
(i)
May 2011 - Wood density (g cm-3)
Sept 2010 - Wood density (g cm-3)

Appendix S1. Comparison of growth rate and trait values of adults and saplings for each of the study species (Table 1). For trait data each data point represents the mean of *ca.* five replicates (see Methods). In each panel the 1:1 line is shown in black. There were insufficient data to calculate growth rates for saplings of *Acacia difficilis* and *Grevillea decurrens*, so in panel (a) these are shown with GR = 0. September 2010 = dry season; May 2011 = wet season.


(a)
Sep 2010
May 2011
y = x
Adult growth rate (cm y-1)
Sapling growth rate (cm y-1)
(b)
Adult leaf mass (g)
Sapling leaf mass (g)
(c)
Adult stem mass (g)
Sapling stem mass (g)
(d)
Adult leaf : stem mass ratio
Sapling leaf : stem mass ratio
(e)
Adult leaf : stem allometry
Sapling leaf : stem allometry
(f)
Adult specific leaf area (cm2 g-1)
Sapling specific leaf area (cm2 g-1)
(g)
Adult Nmass (%)
Sapling Nmass (%)
(h)
Adult Pmass (%)
Sapling Pmass (%)
(i)
Adult wood density (g cm-3)
Sapling wood density (g cm-3)
(j)
Adult Asat (μmol m-2 s-1)
Sapling Asat (μmol m-2 s-1)
(k)
Adult leaf d13C (‰)
Sapling leaf d13C (‰)
(l)
Adult gs (mmol m-2 s-1)
Sapling gs (mmol m-2 s-1)

Appendix S2. Comparison of trait values between the two seasons sampled (wet season, May 2011; dry season September 2010) for both adults (orange circles) and saplings (purple triangles) of 17 species. Points represent species-mean values calculated from *ca*. five individual plants (see Methods). In each panel the 1:1 line is shown in black. 'Wood' density measurements in 2010 (dry season) included bark and sapwood. Repeating this in 2011 (wet season) we removed the bark, giving the density of sapwood only (and in most cases higher values).


(a)
May 2011 - leaf mass (g)
Sept 2010 - leaf mass (g)
(b)
May 2011 - stem mass (g)
Sept 2010 - stem mass (g)
(c)
Adults
Saplings
y = x
May 2011 - LM:SM ratio
Sept 2010 - LM:SM ratio
(d)
May 2011 - LM:SM allometry
Sept 2010 - LM:SM allometry
(e)
May 2011 - SLA (cm-2 g-1)
Sept 2010 - SLA (cm-2 g-1)
(f)
May 2011 - Nmass (%)
Sept 2010 - Nmass (%)
(g)
May 2011 - Pmass (%)
Sept 2010 - Pmass (%)
(h)
May 2011 - d13C (‰)
Sept 2010 - d13C (‰)
(i)
May 2011 - Wood density (g cm-3)
Sept 2010 - Wood density (g cm-3)

APPENDIX S3. Growth rate and trait data used in this study.

Species	age	date	GR (cm yr^{-1})	SLA (cm^2 g^{-1})	leaf N (%)	leaf N (g m^{-2})	leaf P (%)	leaf P (g m^{-2})	A_{sat} (mmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	leaf $d^{13}C$	Leaf mass (g)	Stem mass (g)	LM:SM (g g^{-1})	LA:SM (cm^2 g^{-1})	a_LMSM	Wood density (g cm^{-3})	Bark fraction (%)
Acacia difficilis	ad	May'11	1.56	105.5	2.04	1.93	0.091	0.086	25.61	1087	-29.56	14.7	6.2	2.87	302.2	0.959	0.608	22.5
Acacia difficilis	ad	Sept'10	1.56	88.5	1.56	1.76	0.054	0.061			-30.31	17.8	11.8	1.55	137.1	0.970	0.590	
Acacia difficilis	sap	May'11		110.2	2.45	2.22	0.086	0.078	22.34	882	-29.85	13.1	9.1	1.55	171.2	0.778	0.547	24.4
Acacia latescens	ad	May'11	0.50	68.2	1.88	2.76	0.057	0.083	16.13	530	-30.09	52.1	36.0	1.58	107.5	0.834	0.698	39.6
Acacia latescens	ad	Sept'10	0.50	83.9	2.24	2.67	0.056	0.067			-30.93	23.8	12.9	2.00	167.6	0.888	0.562	
Acacia latescens	sap	May'11	0.78	62.9	1.66	2.63	0.044	0.071	18.50	656	-29.84	31.2	22.0	1.40	88.1	1.122	0.654	44.8
Acacia latescens	sap	Sept'10	0.78	86.8	2.10	2.42	0.062	0.071			-31.13	29.7	13.2	2.22	192.7	0.923	0.583	
Acacia mimula	ad	May'11	0.36	70.7	1.92	2.71	0.067	0.095	17.29	645	-28.26	35.0	25.5	1.88	132.6	0.701	0.691	52.6
Acacia mimula	ad	Sept'10	0.36	71.7	2.19	3.05	0.040	0.055			-30.06	37.8	30.4	1.25	89.6	0.673	0.669	
Acacia mimula	sap	May'11	0.50	63.0	1.90	3.01	0.053	0.085	17.42	682	-28.65	31.8	19.3	1.78	112.0	0.847	0.726	47.0
Acacia mimula	sap	Sept'10	0.50	67.8	2.07	3.06	0.034	0.051			-29.59	29.3	17.5	1.76	119.3	0.796	0.626	
Buchanania obovata	ad	May'11	0.35	51.5	0.49	0.95	0.078	0.152	13.08	354	-27.07	214.1	207.8	1.03	53.0	0.526	0.508	62.5
Buchanania obovata	ad	Sept'10	0.35	57.7	0.99	1.71	0.073	0.127			-28.05	98.3	77.0	1.28	73.7	0.460	0.386	
Buchanania obovata	sap	May'11	0.41	57.1	0.28	0.50	0.067	0.118	11.61	301	-28.05	60.4	76.2	0.88	50.1	0.640	0.394	60.1
Buchanania obovata	sap	Sept'10	0.41	61.0	0.74	1.21	0.056	0.092			-29.65	69.7	125.7	0.55	33.6	0.473	0.377	
Cochlospermum fraseri	ad	May'11	0.53	173.1	1.08	0.62	0.091	0.052	13.39	350	-27.94	31.8	26.8	1.15	199.2	0.516	0.426	48.5
Cochlospermum fraseri	sap	May'11	0.55	168.6	1.90	1.13	0.102	0.061	18.85	642	-28.28	32.5	29.1	1.22	205.5	0.548	0.361	55.9

Corymbia bleeseri	ad	May'11	0.37	53.5	0.89	1.67	0.051	0.096	21.67	1161	-28.71	40.3	44.1	0.87	46.8	0.771	0.716	39.8
Corymbia bleeseri	ad	Sept'10	0.37	60.4	0.86	1.43	0.043	0.071			-29.69	78.8	54.5	1.43	86.2	0.656	0.629	
Corymbia bleeseri	sap	May'11	0.37	47.1	0.83	1.76	0.048	0.102	19.10	467	-27.68	56.6	76.1	0.70	32.8	0.838	0.710	37.7
Corymbia bleeseri	sap	Sept'10	0.37	58.7	0.70	1.19	0.047	0.080			-29.28	60.5	47.5	1.25	73.5	0.742	0.598	
Corymbia porrecta	ad	May'11	0.55	52.5	0.89	1.69	0.044	0.084	20.21	501	-29.33	51.2	78.5	0.64	33.5	0.764	0.681	53.9
Corymbia porrecta	ad	Sept'10	0.55	67.0	0.70	1.05	0.049	0.073			-28.65	91.4	63.8	1.54	102.9	0.707	0.571	
Corymbia porrecta	sap	May'11	0.67	45.9	0.86	1.87	0.044	0.096	21.22	612	-28.64	77.1	82.4	0.94	43.1	0.716	0.641	48.3
Corymbia porrecta	sap	Sept'10	0.67	69.7	0.78	1.12	0.047	0.068			-29.42	61.7	45.4	1.57	109.8	0.767	0.596	
Erythrophleum chlorostachys	ad	May'11	0.38	95.6	1.68	1.75	0.080	0.084	16.16	362	-28.10	88.7	87.0	1.13	108.4	0.542	0.732	53.8
Erythrophleum chlorostachys	ad	Sept'10	0.38	99.7	1.74	1.75	0.060	0.060			-30.93	58.1	96.8	0.61	60.6	0.463	0.449	
Erythrophleum chlorostachys	sap	May'11	0.50	98.0	1.66	1.70	0.078	0.079	17.91	449	-27.77	42.1	25.9	1.71	167.6	0.563	0.651	46.7
Erythrophleum chlorostachys	sap	Sept'10	0.50	95.4	1.85	1.94	0.052	0.055			-30.38	58.5	56.3	1.23	117.0	0.488	0.519	
Eucalyptus miniata	ad	May'11	0.61	68.1	0.74	1.08	0.090	0.132	24.54	744	-29.75	136.8	99.3	1.42	96.8	0.811	0.526	38.6
Eucalyptus miniata	ad	Sept'10	0.61	53.7	0.87	1.62	0.047	0.087			-30.71	83.9	69.3	1.19	63.9	0.814	0.523	
Eucalyptus miniata	sap	May'11	0.70	56.7	0.53	0.93	0.070	0.123	25.24	900	-29.14	112.0	81.8	1.47	83.2	1.001	0.557	32.5
Eucalyptus miniata	sap	Sept'10	0.70	56.4	0.76	1.35	0.040	0.071			-30.35	92.5	57.8	1.73	97.8	0.941	0.495	
Eucalyptus tetrodonta	ad	May'11	0.48	42.9	0.56	1.30	0.037	0.086	17.10	547	-27.75	92.3	52.2	1.76	75.5	0.712	0.621	38.2

Eucalyptus tetrodonta	ad	Sept'10	0.48	51.7	0.78	1.52	0.043	0.083			-27.85	77.4	48.5	1.52	78.4	0.708	0.551	
Eucalyptus tetrodonta	sap	May'11	0.50	42.2	0.50	1.19	0.044	0.104	19.38	613	-28.55	73.8	31.0	2.19	92.3	1.135	0.698	37.1
Eucalyptus tetrodonta	sap	Sept'10	0.50	57.0	0.89	1.55	0.044	0.078			-29.23	43.4	28.1	1.60	91.0	0.721	0.532	
Grevillea decurrens	ad	May'11	0.43	101.8	0.83	0.82	0.051	0.050	14.49	411	-28.41	51.1	38.1	1.53	155.5	0.844	0.607	34.3
Grevillea decurrens	ad	Sept'10	0.43	121.5	0.97	0.80	0.064	0.053			-29.64	36.0	44.9	0.80	97.8	0.722	0.499	
Grevillea decurrens	sap	May'11		98.6	0.87	0.88	0.052	0.052	12.65	329	-27.47	66.8	50.2	1.78	175.8	0.927	0.611	34.2
Grevillea decurrens	sap	Sept'10		113.2	1.05	0.93	0.072	0.064			-29.76	38.3	27.7	1.55	175.5	0.999	0.503	
Grevillea pteridifolia	ad	May'11	0.81	56.2	0.65	1.15	0.045	0.080	18.21	789	-29.52	71.8	42.8	2.23	125.5	0.905	0.584	39.0
Grevillea pteridifolia	ad	Sept'10	0.81	46.5	0.76	1.64	0.056	0.120			-28.80	117.5	48.0	2.55	118.8	0.854	0.486	
Grevillea pteridifolia	sap	May'11	1.00	67.5	0.70	1.03	0.044	0.066	19.72	866	-28.66	71.6	19.2	3.74	252.7	1.076	0.531	35.0
Grevillea pteridifolia	sap	Sept'10	1.00	65.3	0.78	1.19	0.055	0.085			-29.99	107.9	33.1	3.46	226.1	0.916	0.459	
Lophostemon lactifluus	ad	May'11	0.42	90.3	0.90	1.00	0.065	0.072	17.81	541	-29.11	124.7	106.9	1.23	110.8	0.581	0.553	44.2
Lophostemon lactifluus	ad	Sept'10	0.42	69.5	0.89	1.28	0.056	0.081			-31.12	53.3	93.2	0.59	41.2	0.683	0.497	
Lophostemon lactifluus	sap	May'11	0.42	73.5	0.88	1.20	0.061	0.084	20.70	1268	-28.66	50.0	33.2	2.11	154.9	0.528	0.531	37.2
Lophostemon lactifluus	sap	Sept'10	0.42	61.6	0.77	1.25	0.038	0.062			-30.46	32.4	33.1	1.00	61.7	0.458	0.457	
Persoonia falcata	ad	May'11	0.25	61.4	0.43	0.70	0.053	0.086	18.73	762	-29.83	47.6	76.2	0.70	43.3	0.535	0.597	38.9
Persoonia falcata	ad	Sept'10	0.25	70.3	0.86	1.22	0.059	0.084			-31.53	50.2	49.5	1.08	76.2	0.729	0.544	
Persoonia falcata	sap	May'11	0.50	62.0	0.52	0.84	0.056	0.091	17.51	747	-30.29	42.9	62.8	0.66	41.1	0.517	0.594	31.0

Persoonia falcata	sap	Sept'10	0.50	57.7	0.96	1.66	0.044	0.076			-31.94	40.4	47.0	0.87	50.1	0.504	0.480	
Petalostigma pubescens	ad	May'11	0.27	86.6	1.04	1.20	0.060	0.069	12.38	392	-28.59	31.6	30.8	1.09	94.3	0.864	0.668	43.8
Petalostigma pubescens	ad	Sept'10	0.27	96.4	0.67	0.70	0.034	0.035			-30.66	40.7	51.1	0.95	91.6	0.713	0.632	
Petalostigma pubescens	sap	May'11	0.44	74.5	1.10	1.48	0.060	0.080	18.34	443	-28.56	42.4	23.6	1.82	135.8	0.831	0.640	34.8
Petalostigma pubescens	sap	Sept'10	0.44	90.5	0.77	0.86	0.036	0.039			-30.38	22.7	44.3	0.56	50.6	0.642	0.633	
Planchonia careya	ad	May'11	0.42	76.3	1.06	1.38	0.079	0.104	17.19	700	-27.31	83.9	72.9	1.26	96.5	0.563	0.513	47.2
Planchonia careya	ad	Sept'10	0.42	89.5							-28.72	54.7	58.4	0.94	83.9	0.526		
Planchonia careya	sap	May'11	0.40	77.8	0.91	1.17	0.075	0.096	15.45	454	-27.25	46.6	34.4	1.58	123.3	0.659	0.522	43.8
Xanthostemon paradoxus	ad	May'11	0.35	74.6	0.43	0.57	0.054	0.072	14.64	338	-27.28	66.6	110.5	0.59	43.7	0.515	0.656	62.2
Xanthostemon paradoxus	ad	Sept'10	0.35	70.2	0.72	1.02	0.046	0.066			-28.10	25.7	118.9	0.22	15.4	0.472	0.464	
Xanthostemon paradoxus	sap	May'11	0.40	79.2	0.43	0.54	0.063	0.079	16.23	537	-28.12	66.0	71.6	1.30	102.5	0.624	0.584	54.5
Xanthostemon paradoxus	sap	Sept'10	0.40	65.7	0.63	0.95	0.046	0.071				22.0	44.7	0.59	38.7	0.638	0.457	

Appendix 4. Phylogenetic analysis

Editors and reviewers sometimes request authors apply "phylogenetic" analyses to their trait datasets in order to "correct" for the degree of relatedness among species. The idea here is that phylogenetic relatedness is a nuisance that needs to be, and can be, statistically controlled (Felsenstein 1985; Harvey and Pagel 1991). Others take a different view (Uyeda *et al.* 2018; Westoby *et al.* 1998; Westoby *et al.* 1995), viewing phylogenetic and "cross-species" analyses as complementary approaches that ask subtly different questions. A cross-species analysis asks (in this case) whether variation in growth rates of species that occur today in savanna vegetation can be understood as being driven more or less by particular plant traits. For that question, every species is an independent statistical replicate, irrespective or what phylogenetic structure connects them: they are each an independent item of evidence for what types of traits and growth rates are successful in that situation. By contrast, a phylogenetic analysis can be used to ask the question "*Have evolutionary divergences in growth rate and in trait X been associated with one another throughout evolutionary history, more often than expected by chance alone?*". For this reason, phylogenetic methods are sometimes referred to as "correlated divergence" analyses (Moles *et al.* 2005; Westoby *et al.* 1998).

Here we ran a simple correlated divergence analysis based on phylogenetically independent contrasts or PICs (Harvey and Pagel 1991). First, a phylogeny was constructed that described the hypothesised evolutionary relationships among the 17 species (Fig. S3). Tree macro-topology was based on information from Angiosperm Phylogeny Website (www.mobot.org/MOBOT/research/APweb/) version 14 (July 2017). Within-Myrtaceae relationships were derived from (Wilson *et al.* 2001), and within-*Acacia* relationships were resolved with tribe-level information from www.worldwidewattle.com. Second, trait and growth rate (GR) values were calculated for each internal node as the arithmetic average of the trait values for the two daughter species or nodes originating from that node. Third, the set of PICs (divergences) was calculated, each contrast being the difference between the trait (or GR) values for the two nodes or species descending from the contrast-node. (The direction of subtraction in calculating contrasts is unimportant, providing all traits are treated in the same manner). A correlation coefficient was then calculated between the set of GR contrasts and those for each trait (Table S1), assuming N-1 degrees of freedom (Harvey and Pagel 1991) where N is the number of internal nodes providing contrasts (in this case 16).

Figure S3. Hypothesised phylogenetic relationships among the 17 study species

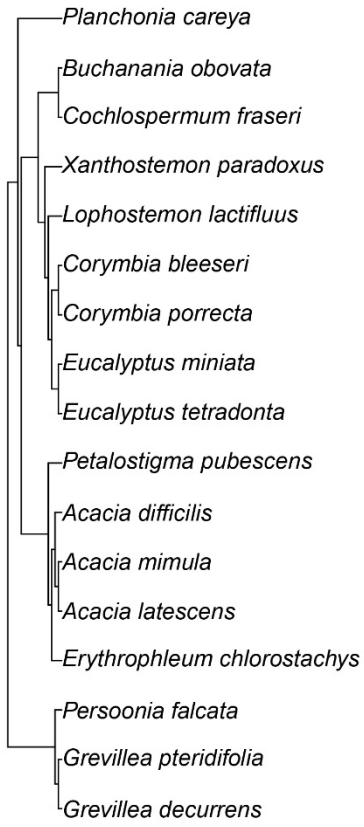


Table S1. Phylogenetically independent contrast analysis of stem diameter growth rates in relation to six plant functional traits.

Trait	*r*	*P*
LMSM80	**0.793**	**0.0001**
a_LMSM	**0.568**	**0.017**
SLA	0.227	0.380
WD	-0.369	0.145
A_{sat}	**0.703**	**0.002**
bark%	**-0.613**	**0.009**

From these results one can see that when considering the matter as evolutionary divergences the conclusion remains that variation in stem diameter growth rate is clearly connected to variation in leaf:stem allometry (LMSM80; a_LMSM) and in photosynthetic rate (A_{sat}), but not to variation in SLA or wood density (WD). In this analysis, divergences in growth rate

were negatively correlated with those in fractional bark allocation – a result we reported with some caution in the cross-species results, since it seemed potentially heavily influenced by *Acacia difficilis* (fast growth rate; very thin bark). The PIC analysis suggests that result was in fact more robust than we suspected.

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